

EXCEPTIONALLY PRESERVED FOSSILS FROM THE SILICA  
SHALE LAGERSTÄTTE (MIDDLE DEVONIAN) OF OHIO,  
MICHIGAN, AND INDIANA: XCT REVEALS DETAILED  
ANATOMICAL INFORMATION

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By

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A handwritten signature in cursive script, reading "Loren E. Babcock". The signature is written in dark ink and is positioned above a horizontal line.

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## TABLE OF CONTENTS

Abstract.....	iii
Acknowledgments.....	iv
List of Figures.....	v
List of Tables.....	vi
Introduction.....	1
Geologic Setting.....	4
Methods	
Specimens.....	5
XCT Scanning.....	5
Analysis.....	5
3D Modeling and Printing.....	5
Results	
Trilobites.....	6
Rugose Corals.....	10
Brachiopods.....	12
Trace Fossils.....	20
Discussion	
The Silica Shale as a Konservat-lagerstätte.....	22
Trilobites.....	22
Rugose Corals.....	23
Brachiopods.....	23
Trace Fossils.....	23
Situs Inversus in <i>Paraspirifer</i> .....	24
Limitations of Using XCT to Study Fossils.....	24

Conclusions.....	25
Recommendations for Future Work.....	26
References Cited.....	27



## ABSTRACT

The Silica Shale of northwestern Ohio and adjacent areas of southern Michigan and northeastern Indiana contains a diverse assemblage of Middle Devonian fossils, many of which are preserved in part by pyrite. Body fossils have been collected from the Silica Shale for more than a century, and large collections have been amassed. Study of samples from the Silica Shale using X-ray Computed Tomography (XCT) reveals that internal nonbiomineralized or lightly biomineralized tissues of shelly taxa are commonly replicated by pyrite. Pyritized trace fossils also have been imaged in some layers. XCT scanning reveals the Silica Shale to be a remarkably rich Konservat-lagerstätte, and exceptional preservation by means of pyrite is present in localities stretching across the Silica Shale outcrop belt. Visualization of the internal soft tissues of some organisms has been aided further by 3D printing of digital models generated using XCT scans.

With XCT, the internal soft tissues of trilobites, brachiopods, and corals have been imaged, and fine details have emerged in many specimens. Pyrite replication seems to have begun quickly after the death of many organisms present in the Silica Shale. Many enrolled trilobites (*Phacops*) have preserved digestive systems, although preserved guts are rare in outstretched trilobites. This suggests that enrolled specimens were corpses, whereas most outstretched trilobites were probably molts. Many brachiopods show preserved brachidia and lophophores, and a few have pyritized muscles and organs. One remarkable example of *Paraspirifer* shows situs inversus of the brachidia, a condition previously unreported in fossil brachiopods. Rugose corals have pyritized structures resembling mesenteries.

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Most importantly, I thank my Mom and Dad for their unwavering support for me as I pursue my goals. They have encouraged me since the first time I said I wanted to be a paleontologist, long before I could even spell the word.

## LIST OF FIGURES

1. Map of Silica Shale exposures
2. Stratigraphic section of Silica Shale
3. XCT scan of two outstretched *Phacops*
4. XCT scan of enrolled *Phacops* with no pyritized tissues
5. XCT scan of enrolled *Phacops* with pyritized gut
6. XCT scan of *Heliophyllum halli*
7. XCT scan of *Pseudatrypa devoniana*
8. XCT scan of *Paraspirifer bownockeri* with no pyritized tissues
9. XCT scan of *Paraspirifer bownockeri* with spiralia preserved
10. XCT scan of *Paraspirifer bownockeri* with spiralia and other organs preserved
- 11a. XCT scan of *Paraspirifer bownockeri* with situs inversus
- 11b. 3D rendering of *Paraspirifer bownockeri* with situs inversus
- 11c. 3D print of *Paraspirifer bownockeri* with situs inversus
12. XCT scan of pyritized trace fossils

## **LIST OF TABLES**

1. Preservation in trilobite specimens
2. Preservation in rugose coral specimens
3. Preservation in brachiopod specimens
4. Preservation by source
5. Summary of preservation in trilobites
6. Summary of preservation in rugose corals
7. Summary of preservation in brachiopods

## INTRODUCTION

The purpose of this study was to explore the pyrite bearing fossils of the Silica Shale for evidence of exceptional preservation using nondestructive X-ray Computed Tomography (XCT) sensing and computational analysis. This method would provide a nondestructive tool to analyze the internal structure of the fossils. The specimens examined in this study include trilobites, brachiopods and rugose corals. The pyritized samples of the Silica Shale have not been previously investigated for exceptional preservation of nonbiomineralized tissues.

The Silica Shale (Stewart, 1927) is a Middle Devonian unit exposed in quarries or other excavations in northwestern Ohio, eastern Indiana, and southern Michigan (e.g., Stewart, 1927; Kesling and Chilman, 1975; Wiedman, 1984, 1985; Figure 1). It consists of interbedded layers of soft, gray, calcareous shale and shaly limestone. This distinguishes it from the hard, underlying limestone (Dundee Limestone) and the overlying dolostone (Ten Mile Creek Dolomite). The Silica Shale has been divided into 27 units with varying lithology and biotas (Kesling and Chilman, 1975; Figure 2). The Silica Shale was deposited approximately 390 million years ago in a tropical, shallow sea formed in the foreland basin of the Acadian Orogenic belt. More argillaceous layers are representative of times of higher sediment influx correlated with greater uplift in the Acadian Mountains to the East. Limestone layers were deposited during times of reduced siliciclastic sediment input. The formation is today, or was historically, exposed in various quarries and other excavations in northwestern Ohio, southern Michigan, and northeastern Indiana (Figure 2).

Grace Anne Stewart (1927) first documented the stratigraphy and fossils of the Silica Shale. Numerous papers have appeared since, including ones by Eldredge, 1972; Green, 1832; Kesling and Chilman, 1975; Klapper and Ziegler, 1967; Stewart, 1936; Stewart and Sweet, 1956; Stumm, 1965; Thorton, 2008; Wiedmann 1984; Wiedman, 1985. The Silica Shale has been widely collected for its incredibly well preserved fossils, which comprise a range of taxa including trilobites, phyllocarids, brachiopods, bryozoans, rugose corals, tabulate corals, crinoids, blastoids, edrioasteroids, cephalopods, gastropods, bivalves, and fishes. The fossils of the Silica Shale have also been observed to be associated with pyrite (Kesling and Chilman, 1975). Despite this long-known association, the formation has not been investigated in detail for exceptional preservation of non-biomineralized tissues.

Pyritization is one common form of exceptional preservation (Cisne, 1973; Allison & Briggs, 1991; Borkow and Babcock, 2003). It is observed in rocks throughout the Phanerozoic, replacing both biomineralized and non-biomineralized parts. The formation of pyrite requires a source of soluble iron and sulfide (Allison and Briggs, 1991). The production of sulfide ions is often facilitated by the metabolism of anaerobic sulfate reducing bacteria. This in turn means that a source of organic carbon is also required to sustain the sulfate reducers. As the bacteria metabolize the carbon, they produce sulfide ions that will readily react with iron to precipitate pyrite or other iron sulfides depending on the relative concentrations of each component.

The process of preserving soft tissues in pyrite is thought to occur quite rapidly after death, within seven to ten days (Borkow and Babcock, 2003). After the organism dies, it must be preserved before it decomposes and disarticulates. An environment with limited organic carbon input is better for the preservation of soft tissues, as this results in a concentration of sulfate reducing bacteria and therefore pyrite around the corpse, and less pyrite in the surrounding sediment. When the carcass has reached the sediment, it is rapidly colonized by sulfate reducing

bacteria that feed on the organic components. The metabolism produces sulfide ions, which react with iron in the water at an incredibly local scale to precipitate pyrite and encrust the soft tissues of the organism, preserving them. Borkow and Babcock (2003) illustrated pyritized bacteria and fungi that likely play a key role in the preservation process associated with exceptionally preserved fossils.

The purpose of this study was to explore the pyrite-bearing fossils of the Silica Shale for evidence of exceptional preservation. If the formation were found to contain a significant number of exceptionally preserved fossils, it then would be better to consider it as a Konservat Lagerstätte – a “rock body unusually rich in paleontological information” (Seilacher et al., 1985). Additionally, this study demonstrated the use of X-ray Computed Tomography as a tool to visualize these structures without destroying or damaging the specimen. Further it demonstrated the use of these scans to create a 3D model of the internal structure of a specimen.

The use of XCT in this study allowed for the non-destructive visualization of the internal structures of the specimens. While this tool has become a staple in the medical field, the full applications of it in paleontology have not been explored. The XCT works particularly well when looking for pyritized soft tissues due to the difference in density between the pyrite preserving soft tissues and the calcite of the limestone rock. The use of XCT eliminates any concerns of accidentally removing paleontologically important features during preparation or damaging the sample in any way. Additionally, the scans can then be used to create 3D models to view the relationship of the structures inside without having to open the fossil. These models can also be printed using a 3D printer.



Figure 1: Map of quarries where the Silica Shale is exposed at the surface.

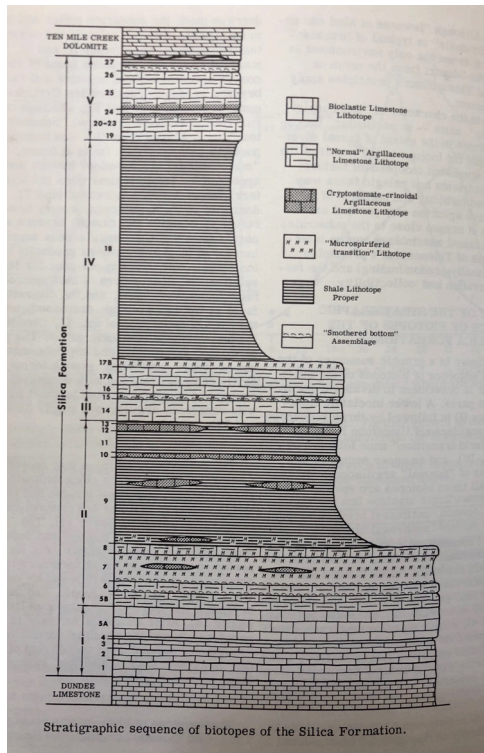


Figure 2: Stratigraphic column of the Silica Shale (from Kesling and Chilman, 1975)

## **GEOLOGIC SETTING**

### **Geology**

The Silica Shale is a Middle Devonian (Givetian) rock unit that is exposed in excavations across Ohio, southern Michigan, and northeastern Indiana. The rock unit consists of interbedded mixed carbonate and fine siliciclastic rocks, both primarily gray in color. The unit was deposited in a shallow subtidal shelf. The depositional area was periodically subjected to storms, indicated by the beds of enrolled trilobites that can be inferred to be storm beds (Babcock and Speyer, 1987). The numerous trace fossils show that the water column was oxygenated. There is pyrite associated with the Silica Shale. Pyritization probably took place in locally dysoxic patches below the sediment-water interface, termed “chemical microenvironments” (Babcock and Speyer, 1987).

The stratigraphy, paleontology, and environmental setting of the Silica Formation have been reviewed by Eldredge, 1972; Green, 1832; Kesling and Chilman, 1975; Klapper and Ziegler, 1967; Stewart, 1927; Stewart, 1936; Stewart and Sweet, 1956; Stumm, 1965; Thorton, 2008; Wiedmann 1984; Wiedman, 1985.



## **METHODS**

### **Specimens**

Most specimens used in this study are in the collections of the Orton Geological Museum at The Ohio State University. These samples were primarily collected from quarries in Silica, Ohio. Additional specimens are from Sylvania, Ohio, and Paulding, Ohio. Some specimens from eastern Indiana were provided for study by Lawrence Wiedman. Initially, over one hundred specimens of trilobites, brachiopods, and rugose corals were inspected for evidence of pyritization. Specimens were examined using a light microscope for visible external pyrite. Additionally, anomalously high mass, correlating with high density, was used to identify fossils with internal pyrite.

### **XCT Scanning**

Some specimens thought to contain pyrite were scanned using X-ray Computed Tomography (XCT). XCT provides a nondestructive method to view the internal structure of specimens. Scans were completed using a portable Neurologica CereTom CT scanner, housed at The Ohio State University. Scans were completed at the maximum resolution of 0.5 by 0.5 by 0.625 mm using a voltage of 120 kV. Some specimens were placed in a container filled with sand to reduce the effects of beam hardening and prevent artifacts. In total, sixty-seven samples were scanned. Some specimens of similar taxa from the Columbus Limestone were also scanned to compare non-pyritized fossils to those of the Silica Shale.

### **Analysis**

The scan data were viewed and analyzed using FIJI software. This program was primarily used to view the scans slice by slice in three orthogonal views. Additional ways in which the images were manipulated include: using pixels to measure lengths, changing look-up tables (LUT) to highlight features of a certain density, generating 3D surface models, and comparing the density of particular areas within the sample using numerical values.

The program Avizo was used to create detailed 3D models of internal features that could be rotated and colored.

### **3D Modeling and Printing**

The scans were then used to construct 3D polygonal models that could be printed. The process to prepare a scan to be 3D printed requires multiple steps (Buckling et al., 2017; Lauridsen et al., 2016). First the scan is segmented, highlighting the portions of interest in the scan that are to be printed. The segmentation process was conducted using the program Seg3D. A rough selection is made using the quantitative values assigned to each pixel in the scan, and then the images are edited by hand one slice at a time. The next step is mesh refinement. This process takes the stack of two-dimensional images and compiles them into a coherent three-dimensional polygonal structure. The program MeshMixer was used to create the stl file that could then be printed. After the file was imported, a smoothing function was applied to reduce the blocky appearance due to the limited voxel size of the scanner. Additionally, holes in the model were fixed by a process of selecting the area around the hole, deleting it, and using the analysis tool to auto-repair these breakages. The final step is to print the object using a 3D printer. In this project, one object was

printed using the LulzBot TAZ 6 printer available at the Digital Union at The Ohio State University. Supports for the model were added by staff at the Digital Union.

## RESULTS

### Trilobites

Specimens of *Phacops rana* (also published as *Eldredgeops rana*) in the Silica Shale are typically found in one of two positions: outstretched or enrolled. Most specimens showed some external pyritization, particularly in the eye facets. Internal soft tissue preservation included the stomach under the glabella, the gut running along the dorsal side of the axial lobe, and possible appendages branching from the axial lobe.

Two of nine outstretched *Phacops rana* scanned showed preserved guts. In both samples only the stomach was preserved.

Eight of nine enrolled *Phacops rana* show some or all of the gut preserved. Four of those eight also appeared to have some limbs preserved.

Figures 3-5 show slices from three example scans of *Phacops*.

Table 1 shows the preservation of features in the enrolled trilobite specimens.

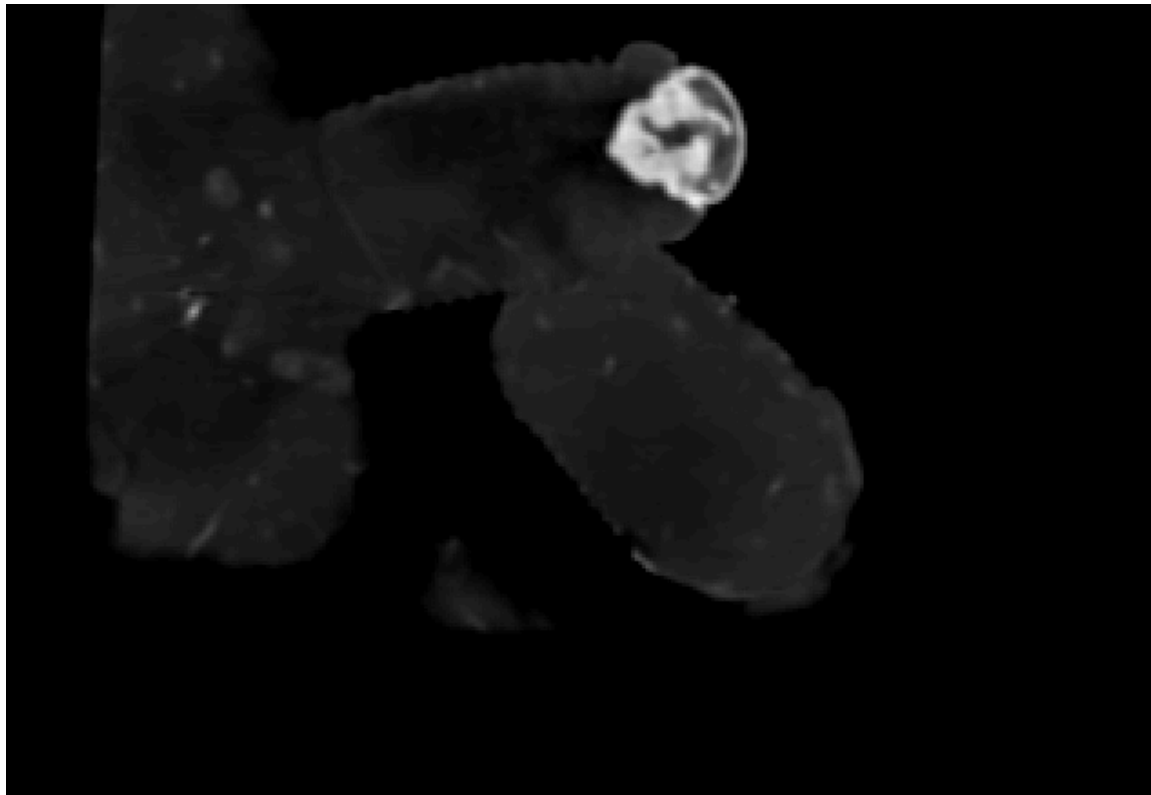


Figure 3: Two outstretched *Phacops* on a single slab. The upper one (as depicted) shows a pyritized crop (stomach), whereas the lower one lacks any internal pyritized structures. Small pyritized trace fossils in the calcareous shale matrix are also evident.

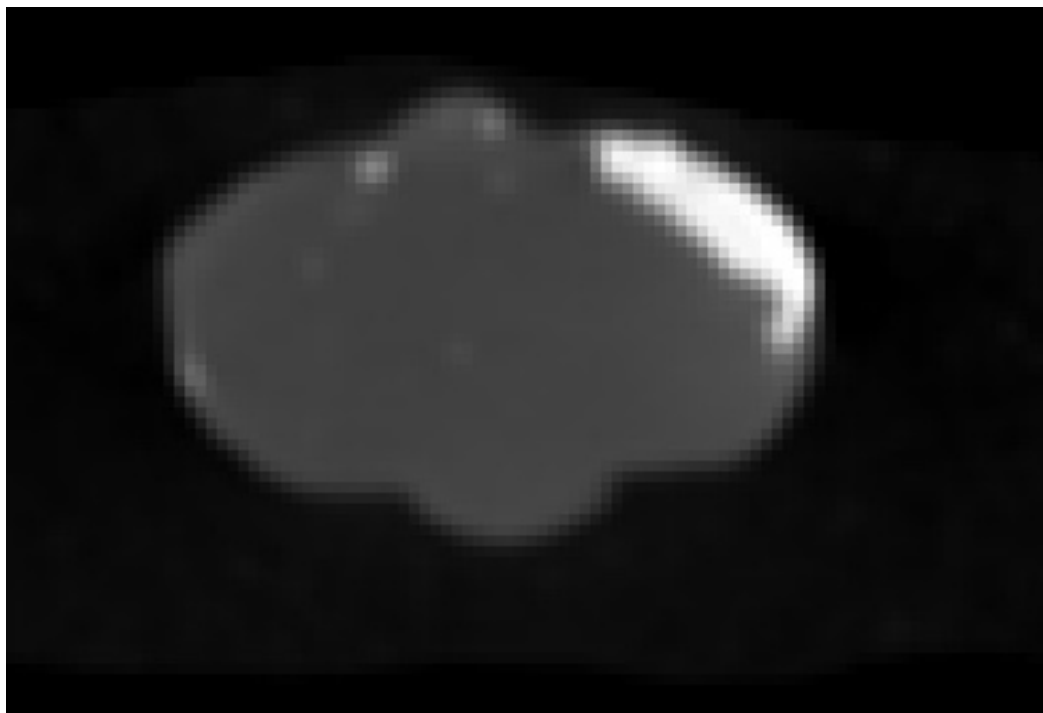


Figure 4: Enrolled *Phacops rana* with no soft tissues preserved in pyrite.



Figure 5: Enrolled *Phacops rana* showing preserved gut along dorsal surface and preserved appendages indicated by spots ventral to gut.

Table 1: Preservation in trilobite specimens

Specimen	Position	Stomach	Gut	Appendages
001	enrolled	x	x	x
002	2 outstretched	x		
003	enrolled	x	x	x
004	outstretched			
009	outstretched			
010	outstretched			
040	enrolled	x	x	
041	enrolled	x	x	
042	enrolled	x	x	
043	enrolled	x	x	
044	enrolled			

<b>045</b>	enrolled	x	x	x
<b>065</b>	outstretched			
<b>066</b>	3 outstretched	x		
<b>067</b>	enrolled	x	x	x
<b>Total</b>	<b>18</b>	<b>10</b>	<b>8</b>	<b>4</b>

## Rugose Corals

Multiple groups of rugose corals were scanned. All groups showed similar patterns of pyritization internally, preserving the septa and other radially symmetric features. Many specimens were pyritized throughout the entire corallum, and not solely at the calyx.

Twelve of twelve *Heliophyllum halli* scanned showed pyritized internal structures resembling mesenteries.

Three of three *Zaphrentis prolifica* scanned showed pyritized internal structures resembling mesenteries.

Figure 6 shows a slice from an example scan of *Heliophyllum halli*.

Table 2 shows the preservation of features in the rugose coral specimens.

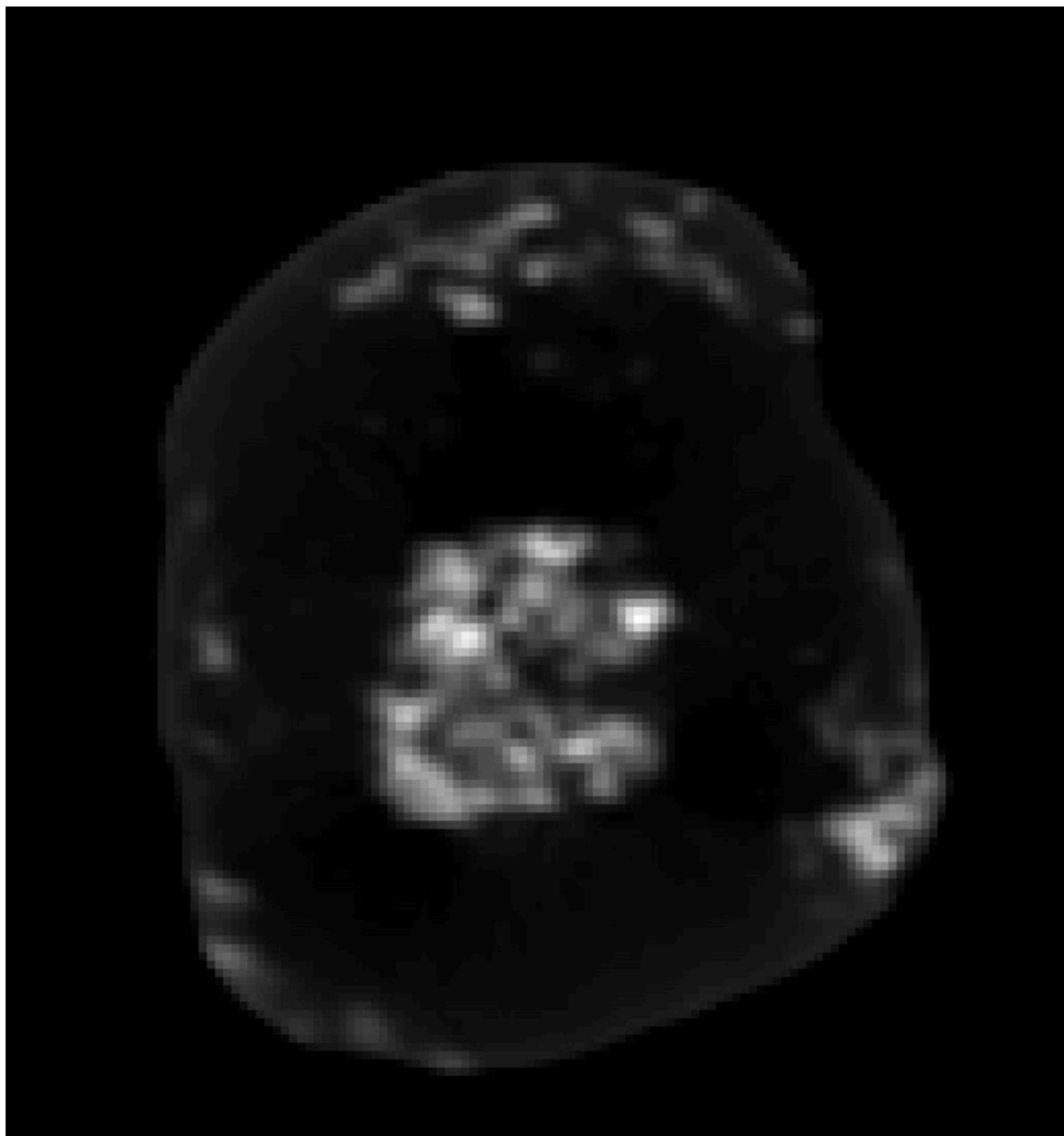


Figure 6: Cross sectional view of *Heliophyllum halli* showing distinct cross-shaped pattern of mesenteries in center.

Table 2: Preservation in rugose coral specimens

Specimen	Taxa	Mesenteries
005	<i>Heliophyllum halli</i>	X
029	<i>Heliophyllum halli</i>	X
030	<i>Heliophyllum halli</i>	X
031	<i>Heliophyllum halli</i>	X
032	<i>Heliophyllum halli</i>	X

<b>033</b>	Heliophylum halli	X
<b>034</b>	Heliophylum halli	X
<b>035</b>	Heliophylum halli	X
<b>036</b>	Heliophylum halli	X
<b>037</b>	Heliophylum halli	X
<b>038</b>	Heliophylum halli	X
<b>039</b>	Heliophylum halli	X
<b>051</b>	Zaphrentis prolifica	X
<b>052</b>	Zaphrentis prolifica	X
<b>053</b>	Zaphrentis prolifica	X
<b>Total</b>	<b>15</b>	<b>15</b>

## Brachiopods

Multiple brachiopod groups were scanned including many specimens of spiriferids. In most samples the spiralia were pyritized and the interior of the valves had a layer of pyrite. In the samples scanned, there was no evidence of the pedicle being preserved. Table 4 shows the preservation of features in the brachiopod specimens.

Three of four *Pseudoatrypa devoniana* scanned showed preserved brachidia. The brachidia appear to be asymmetrical in size, one occupying much more space within the valves than the other. Figure 7 shows a slice from an example of *Pseudoatrypa devoniana*.

Thirteen of fifteen *Paraspirifer bownockeri* scanned showed preserved brachidia. Six of these thirteen also have further pyritization that may preserve internal tissues including paired muscles, the stomach, or the pedicle. All fifteen specimens had pyrite lining some or all of the interior of both valves. This may represent pyritization of mantle tissue. Figures 8-11 show a slice from four example scans of *Paraspirifer bownockeri*.

Seven of nine *Mucrospirifer mucronatus* scanned showed preserved brachidia, and all nine specimens had pyrite lining the interior of the valves.

Two of two *Spirifer euryteines* scanned showed pyrite lining the interior of the valves and preserved brachidia, although in both specimens the brachidia appear to have shifted position after death.

Three of three *Mediospirifer audaculus* showed pyrite lining the interior of the valves and preserved brachidia. One of the three specimens also appears to have other pyritized internal tissues.



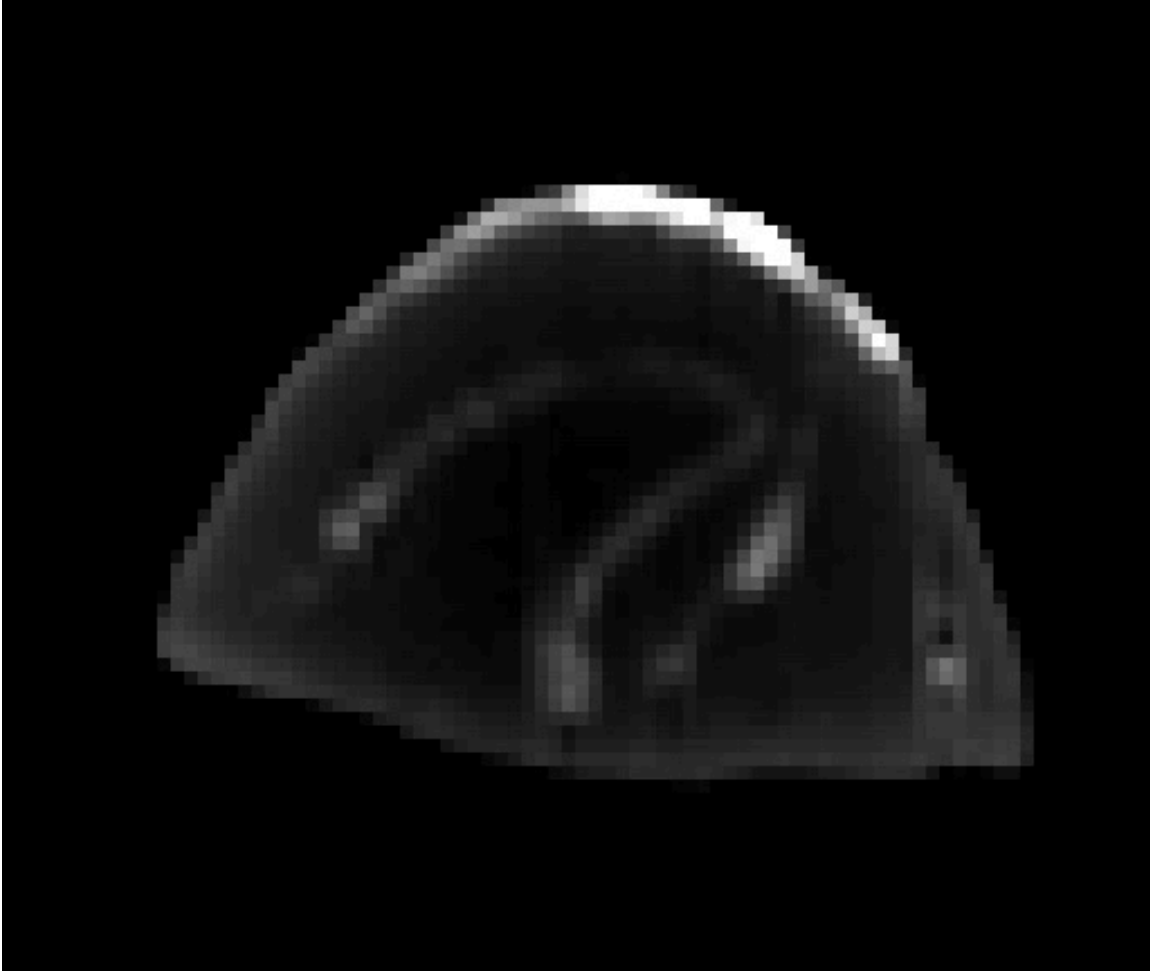


Figure 7: *Pseudoatrypa devoniana* with asymmetrical pyritized brachidia.

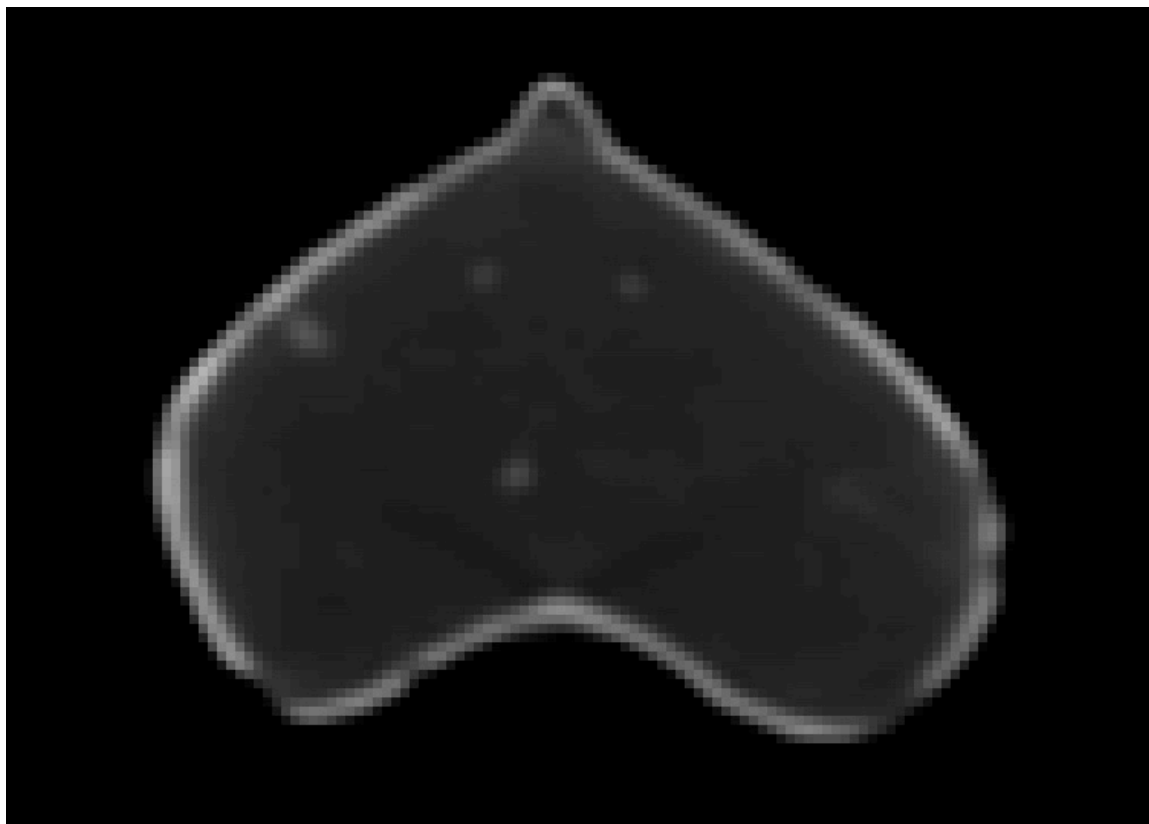


Figure 8: *Paraspirifer bownockeri* with a pyrite layer inside shell, perhaps pyritized mantle.

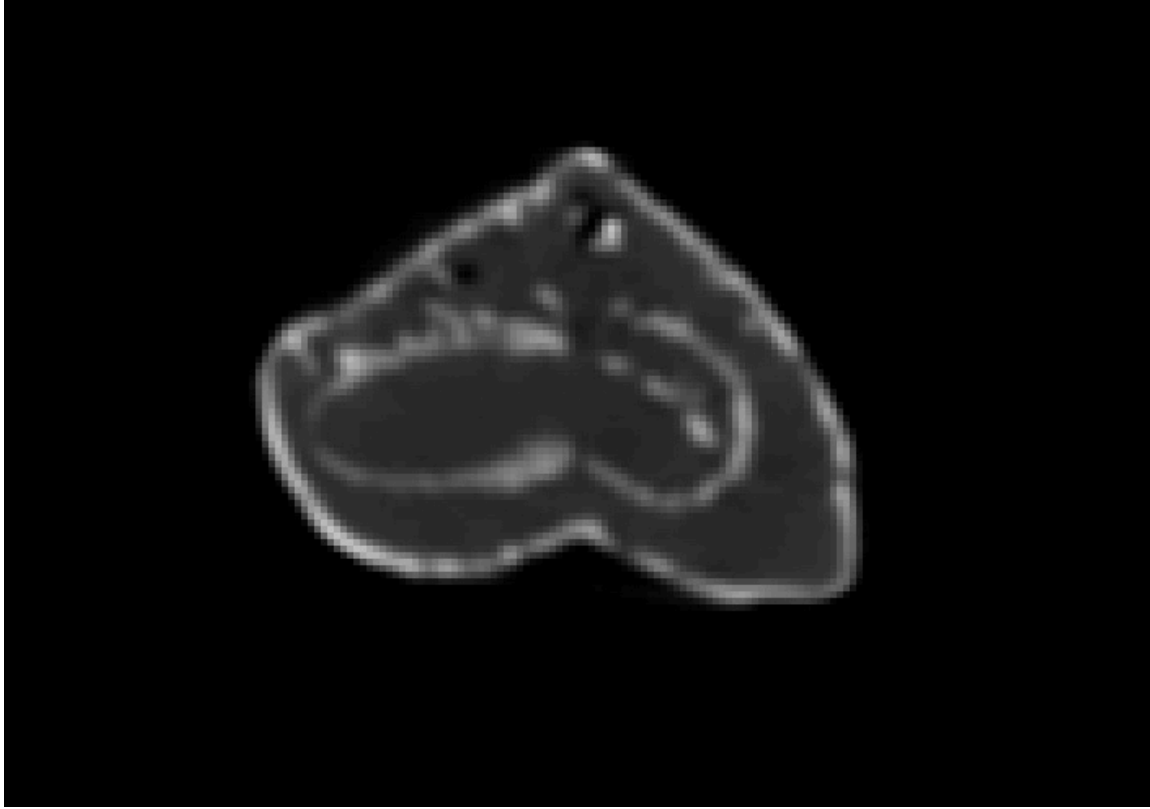


Figure 9: *Paraspirifer bownockeri* showing pyritized brachidia, including filaments along the lophophores, and pyrite lining the insides of the valves.



Figure 10: *Paraspirifer bownockeri* with pyritized brachidia as well as other pyrite masses that may be soft tissues including the muscles, stomach, or pedicle. It also shows pyrite lining both valves.

Table 4: Preservation in brachiopod specimens

Specimen	Taxa	Spiralia	Valves	Pedicle	Further Pyritization
006	<i>Pseudatrypa devoniana</i>	X	X		
046	<i>Pseudatrypa devoniana</i>		X		
047	<i>Pseudatrypa devoniana</i>	X	X		
048	<i>Pseudatrypa devoniana</i>	X	X		
007	<i>Paraspirifer bownockeri</i>	X	X		
008	<i>Paraspirifer bownockeri</i>		X		
011	<i>Paraspirifer bownockeri</i>	X	X		X
012	<i>Paraspirifer bownockeri</i>	X	X		X
013	<i>Paraspirifer bownockeri</i>	X	X		
014	<i>Paraspirifer bownockeri</i>	X	X		X
015	<i>Paraspirifer bownockeri</i>	X	X		X
016	<i>Paraspirifer bownockeri</i>	X	X		X

<b>017</b>	Paraspirifer bownockeri		X		
<b>056</b>	Paraspirifer bownockeri	X	X		
<b>070</b>	Paraspirifer bownockeri	X	X		X
<b>071</b>	Paraspirifer bownockeri	X	X		
<b>072</b>	Paraspirifer bownockeri	X	X		
<b>073</b>	Paraspirifer bownockeri	X	X		
<b>089</b>	Paraspirifer bownockeri	X	X		
<b>018</b>	Mucrospirifer mucronatus	X	X		
<b>019</b>	Mucrospirifer mucronatus		X		
<b>020</b>	Mucrospirifer mucronatus	X	X		
<b>021</b>	Mucrospirifer mucronatus	X	X		
<b>022</b>	Mucrospirifer mucronatus		X		
<b>023</b>	Mucrospirifer mucronatus	X	X		
<b>024</b>	Mucrospirifer mucronatus	X	X		
<b>025</b>	Mucrospirifer mucronatus	X	X		
<b>026</b>	Mucrospirifer mucronatus	X	X		
<b>054</b>	Spirifer euryteines	X	X		
<b>055</b>	Spirifer euryteines	X	X		
<b>057</b>	Mediospirifer audaculus	X	X		X
<b>058</b>	Mediospirifer audaculus	X	X		
<b>059</b>	Mediospirifer audaculus	X	X		
<b>Total</b>	<b>33</b>	<b>28</b>	<b>33</b>	<b>0</b>	<b>7</b>

One specimen of *P. bownockeri* exhibits situs inversus of the spiralia (Figures 11a–11c), a condition in which both spiralia open to the same side of the body rather than being symmetrical about the medial line. The spiralia are still fully intact and connected to the brachial valve, indicating this was the position of the body in life, and related to taphonomic processes. Situs inversus has not been previously documented in any brachiopod. Figure 11a shows a scan of the *Paraspirifer* specimen with situs inversus. Figure 11b shows a 3D rendering of the specimen. Figure 11c shows a 3D printed model of the specimen.

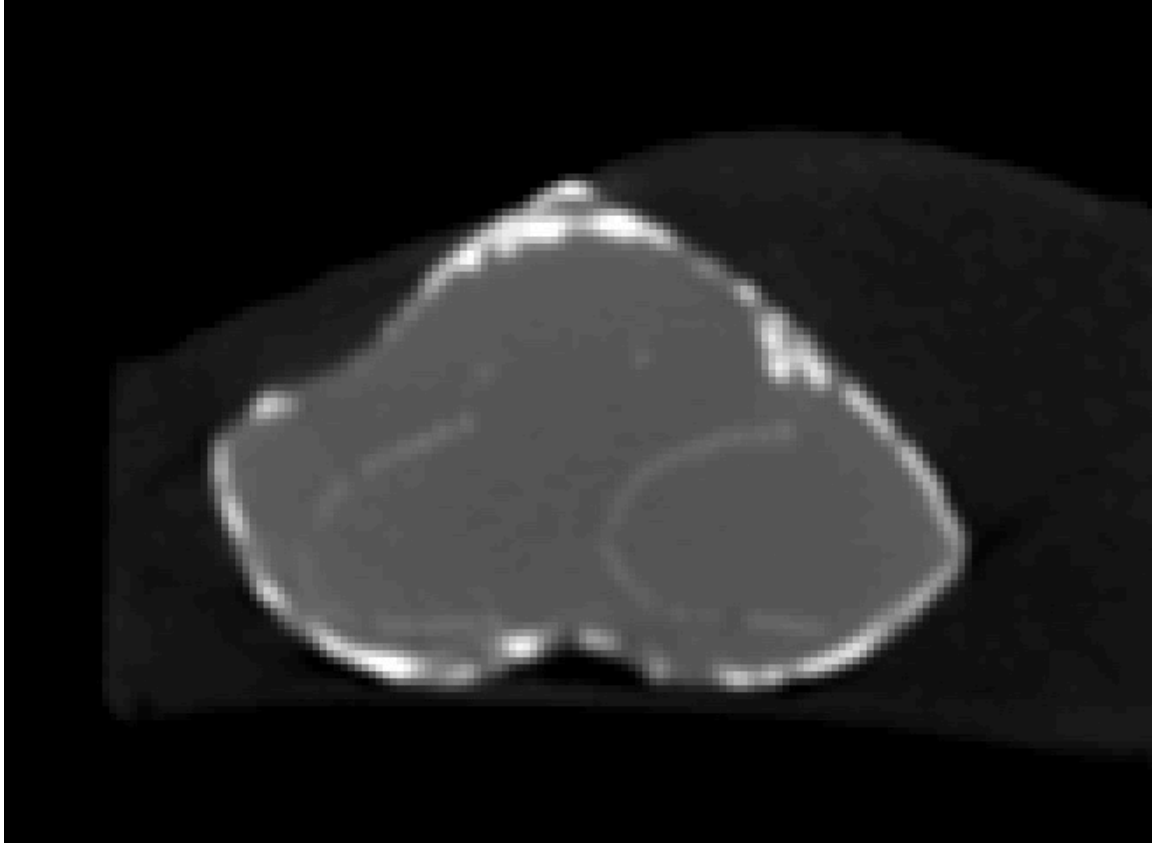


Figure 11a: *Paraspirifer bowockeri* with situs inversus; both spiralia open to the same side. These spiralia are still in place and attached to the brachial valve.

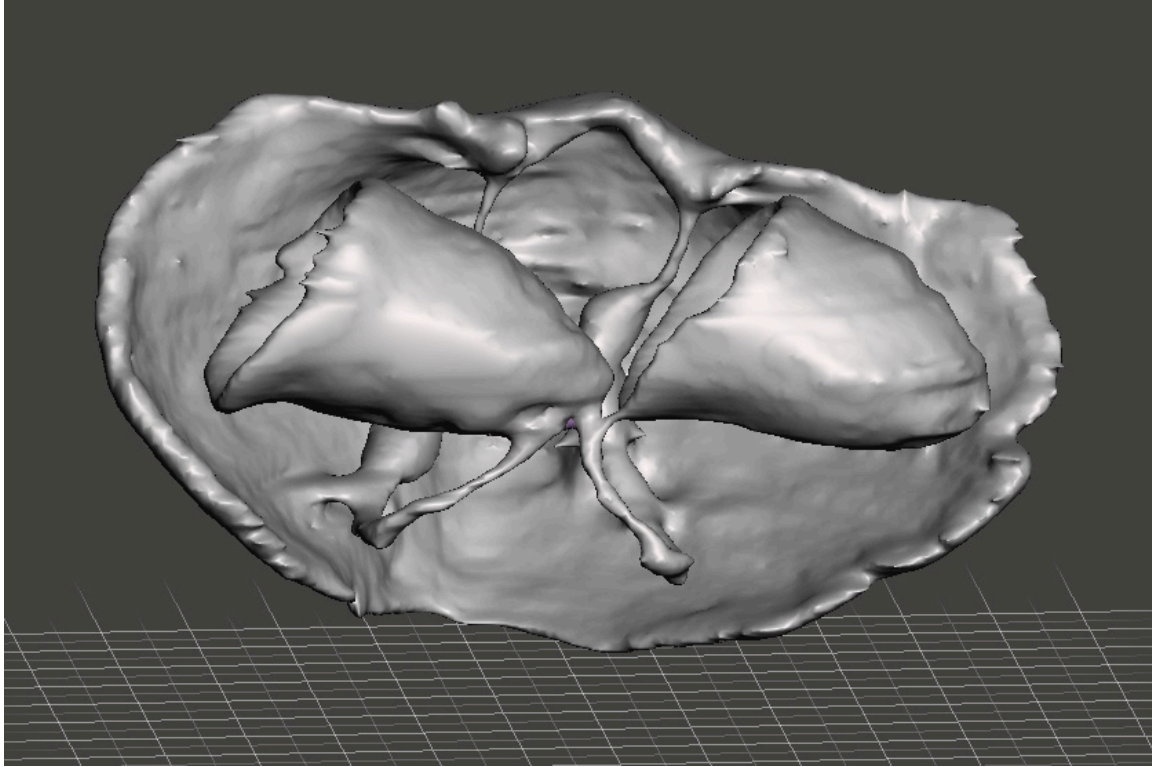


Figure 11b: 3D rendering of a specimen of *Paraspirifer bownockeri* with situs inversus (see Figure 11a).



Figure 11c: 3D printed model of a specimen of *Paraspirifer bownockeri* with situs inversus (see Figure 11a).

### Trace Fossils

Specimens still in matrix showed extensive pyritized burrows. Some burrows extended into the body fossils. In other specimens, the burrows appear to be truncated below the body fossil.

Figure 12 shows a scan of many pyritized burrows.



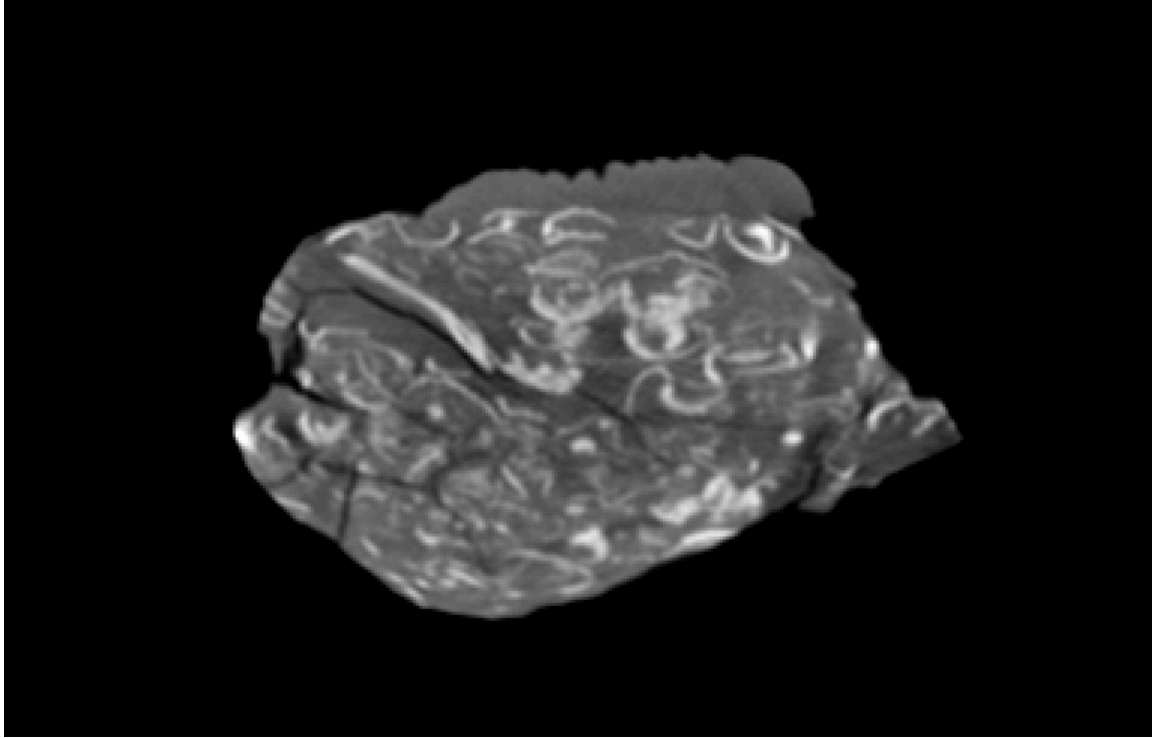


Figure 12: Outstretched *Phacops rana* over well bioturbated, pyritized brachiopod-rich layer. The matrix is full of pyritized burrows and disarticulated brachiopod valves. Note that the bioturbated layer appears to be truncated just below the trilobite.

## DISCUSSION

### The Silica Shale as a Konservat-lagerstätte

The well-preserved, biomineralized fossils of the Silica Shale have been studied for about a century. Now, with the discovery of pyritized non-biomineralized parts, the Silica Shale should be acknowledged as a Konservat-lagerstätte, or deposit of exceptional fossil preservation. So far, more than 81 specimens, comprising eight species assigned to three phyla, as well as trace fossils, have been shown to reveal soft parts. cursory examination of museum specimens indicates that pyritized soft tissues are remarkably abundant in the unit. Table 6 shows how many specimens from each category exhibited preservation. The well-preserved soft tissues in this unit can reveal novel biological and taphonomic information about the biota of this Middle Devonian unit.

Table 6: Preservation by sources and characteristics

Source	Unit	Trilobites	Brachiopods	Rugose Corals	Trace Fossils	Total
<b>Orton Geological Museum</b>	Silica Shale	10/18	28/33	15/15	3/3	<b>56/69</b>
<b>Lawrence Wiedman</b>	Equivalent of Silica Shale in Eastern Indiana	9/9	0	0	0	<b>9/9</b>
<b>Orton Geological Museum</b>	Columbus Limestone	0	0/1	0/2	0	<b>0/3</b>
<b>Total</b>		<b>19/27</b>	<b>28/34</b>	<b>15/17</b>	<b>3/3</b>	<b>65/81</b>

### Trilobites

Trilobites in the Silica Shale are typically preserved either fully outstretched or completely enrolled. Most enrolled specimens showed some degree of exceptional preservation including guts and limbs. These specimens are evidently corpses. The outstretched trilobites typically did not have pyritized soft tissues, and many did not show associated pyritization at all. Most such specimens can be inferred to be molts, as they apparently lacked soft tissues. Table 7 summarizes trilobite preservation by taxa.

Table 7: Preservation in trilobites

Taxa	Eye Facets	Stomach	Gut	Appendages	Total
<b><i>Phacops rana</i> outstretched</b>	9	2	2	0	<b>9</b>
<b><i>Phacops rana</i> enrolled</b>	9	8	8	4	<b>9</b>
<b>Total</b>	<b>18</b>	<b>10</b>	<b>10</b>	<b>4</b>	<b>18</b>

## Rugose Corals

Multiple taxa of rugose coral showed similar forms of internal pyritization. The features preserved resemble radially symmetric mesenteries. Interestingly, the pyritization occurs throughout the corallum and not only at the calyx, where the living organism would have resided. This could have been caused by residual organic material remaining in the calcite structure, or possibly even pyritization occurring while the organism was still alive and was incorporated into the structure. Table 8 summarizes rugose coral preservation by taxa.

Table 8: Preservation in rugose corals

Taxa	Mesenteries	Total
<b>Heliophyllum halli</b>	12	<b>12</b>
<b>Zaphrentis prolifica</b>	3	<b>3</b>
<b>Total</b>	<b>15</b>	<b>15</b>

## Brachiopods

Most of the brachiopod specimens exhibited pyritization. Specimens of many taxa have a layer of pyrite inside the valves. This layer is likely the remains of the mantle that produced the shell. Additionally, many brachiopods had pyritized spiralia, including some remarkable specimens that had individual filaments branching from the spiral structure preserved. Some specimens also had other pyritized features including what appears to be paired muscle sets near the hinge area and a more central organ that could be either the stomach or the pedicle. Table 9 summarizes brachiopod preservation by taxa.

Table 9: Preservation in brachiopods

Taxa	Spiralia	Valves	Pedicle	Further	Total
<b>Pseudoatrypa devoniana</b>	3	4	0	0	<b>4</b>
<b>Paraspirifer bownockeri</b>	13	15	0	6	<b>15</b>
<b>Mucrospirifer mucronatus</b>	7	9	0	0	<b>9</b>
<b>Spirifer euryteines</b>	2	2	0	0	<b>2</b>
<b>Mediospirifer audaculus</b>	3	3	0	1	<b>3</b>
<b>Total</b>	<b>28</b>	<b>33</b>	<b>0</b>	<b>7</b>	<b>33</b>

## Trace Fossils

Among samples still in matrix there were many pyritized burrows. These burrows are clear evidence that the sediment was not permanently anoxic. Nevertheless, dysoxia or anoxia is presumed to be important for pyritization. It is likely that local dysoxia, within so-called chemical microenvironments, was a major contributor to pyritization (Borkow and Babcock, 2003; Ahn & Babcock, 2012). Burrows extending into the body fossils are possible evidence of scavenging behavior. Additionally, in some samples, the burrows appear to be truncated below

the layer containing the body fossil. This could be evidence of a turbidite bed that stripped away the tops of the burrows, and then deposited the layer containing the fossil.

### Situs Inversus in *Paraspirifer*

One particularly interesting specimen of *Paraspirifer bownockeri* had both spiralia opening to the same side of the organism. The connections from the spiral structure to the brachial valve remain totally intact, indicating that this was the orientation of these structures in life and not caused by some taphonomic process. This is the first unambiguous evidence of situs inversus in the Paleozoic fossil record. This organism grew to a large size, demonstrating that this feature was not so impactful on its fitness that it could not survive.

### Limitations of Using XCT to Study Fossils

There were some limitations to this study. The largest limitation was that without breaking open a sample to confirm the results observed in the scans, there is still a level of uncertainty in the results. The specimens used in this study all came from available collections, and extensive preparation was not conducted. Another limitation to this study was the resolution of the scanner. Any features that were smaller than the voxel size of  $0.625 \times 0.625 \times 0.5$  mm would not resolve on the scans. This was good enough for observing large-scale features, such as the gut or brachidia, but could limit detection of finer structures such as details of the appendages of trilobites.

## **CONCLUSIONS**

The Silica Shale contains many exceptionally preserved fossils with pyritized soft tissues. It should be recognized and studied as a Konservat Lagerstätte with an abundance of paleontological, biological, and taphonomic information. Of sixty-seven samples viewed in this study, fifty-six had pyritized soft tissues including guts and appendages in trilobites, lophophores in brachiopods, and mesenteries in rugose corals. Additionally, the first record of a brachiopod fossil exhibiting situs inversus was discovered.

This study also documented the use of XCT as a nondestructive tool to visualize the internal structure of fossil specimens. XCT allowed for the detailed analysis of internal features while preserving the entirety of the specimen. This tool has broad applications to improve the study of paleontology and could reveal additional details preserved in the fossil record.

Pyritization is one form of exceptional preservation known in the fossil record. Many units are known to be associated with pyrite, but have not been studied for exceptional preservation. Pyrite preserving soft tissues may be more common than previously thought, and these fossils should be studied for new paleontological insights.

## **RECOMMENDATIONS FOR FUTURE WORK**

The next step in this study is to collect samples that can be broken open to confirm the results previously found. This would establish XCT as an invaluable tool in studying exceptionally preservation in a non-destructive manor. Further, broken specimens could be examined using a Scanning Electron Microscope (SEM) to observe the fine details of the pyritized structures. Previous studies have used this method to observe preserved fungi and bacteria, the proposed mediators of pyritization, as well as the gut contents of trilobites. Sulfur isotope studies have been conducted on other localities with pyritization to understand the timing of pyritization (Briggs, Bottrell, and Raiswell, 1991). Similar techniques could be applied to the fossils of the Silica Shale. More broadly, other localities that are known to have pyrite should be more closely examined for pyrite preserving non-biomineralized tissues. In these localities, the conditions existed for the precipitation of pyrite, and if those units are fossiliferous, there is a high probability the conditions existed for exceptional preservation to occur.

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